REPRODUCTIVE POTENTIAL OF BROMUS MOLLIS AND AVENA BARBATA UNDER DROUGHT CONDITIONS

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ABSTRACT

In California annual grasslands, flowering and seed set occur during spring when soil water conditions change rapidly due to increased plant growth, high evapotranspiration, and infrequent rainfall. This study simulated short drought periods and an early onset of summer drought to determine possible drought effects on seed production and population carry-over of *Bromus mollis* and *Avena barbata*. Drought treatments diminished seed production, but some germinable seeds were produced under severe conditions. Drought effects carried over to the next generation because stressed plants produced smaller seeds that produced smaller seedlings.

Annual species comprise from 50% to more than 90% of the foliar cover in California annual grasslands. Most of them are introduced annuals, having come from other parts of the world with Mediterranean climates. Success of the alien species has been attributed to abundant seed production (Biswell and Graham 1956), ability to survive summer drought as seed (Bartolome 1976), and ample seed production, even under heavy grazing pressure (Heady 1961).

Major and Pyott (1966) and Bartolome (1979) showed that a majority of the viable seeds produced each spring by winter annuals germinate the following autumn; seed reserves are small as a result. This means that the plants must produce seeds nearly every year. Seed production data have been reported by several workers in the California annual grassland (Papanastasis 1973, Biswell and Graham 1956, Batzli and Pitelka 1970, Holland 1974), but the numbers vary considerably from site to site and year to year. Environmental conditions in California and their direct effects on annual grass reproduction have rarely been reported, making it difficult to compare seed production data. Moreover, knowing the total number of seeds produced is not as important as knowing whether enough germinable seed is produced to carry the vegetation through another year.

In California annual grasslands, flowering and seed set occur in the annuals during spring when soil water conditions change rapidly because of increased plant growth, high evapotranspiration, and infre-

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quent rainfall (Evans et al. 1975). Although seed production insufficient to maintain populations of the alien species has not been observed (Biswell and Graham 1956, Heady 1961), reproduction is probably influenced by spring weather conditions (Ewing 1981). Newman (1967) studied the effects of spring drought periods on reproduction of *Aira praecox* in Great Britain and demonstrated that a short spring drought period did not reduce seed production or seed weight. Only severe drought (soil matric potential below an estimated threshold of −30 bars) caused noticeable differences in inflorescence emergence, seed formation, and seed weight. He concluded that *Aira praecox* is drought resistant beyond what is necessary to reproduce successfully.

Short drought periods during the winter-spring growing season and an early onset of summer drought were simulated in this study to determine possible drought effects on seed production and population carry-over of alien annuals in California annual grasslands.

Methods

Facility. Twelve plywood boxes, 60 × 60 × 60 cm, were filled with a pale brown, medium-textured, and slightly acidic Laughlin (fine-loamy, mixed, mesic Ultic Haploxeroll) soil from an annual grassland, oak-savannah range site at the Hopland Field Station, Mendocino County, California. Drainage was provided through a 10-cm layer of washed gravel under the soil and holes in the bottoms.

After fall germination of winter annuals in the field (14 September 1978), 10-cm deep slabs of sod from the same site were removed and set on top of the soil. Each of the twelve experimental units had continuous plant cover with typical botanical composition for the beginning of the growing season at Hopland.

The experimental units were transported to a field laboratory at the Gill Tract in Albany, California, where a clear plastic shelter with open sides was constructed above them to intercept precipitation. Temperatures under the rain shelter tracked outside temperatures, never varying by more than 1°C. Spectroradiometer readings indicated a complete light spectrum passed through the plastic, though the intensity at all wavelengths was reduced by about 25%. Three gypsum resistance blocks were placed at each of three soil depths, 9, 20, and 40 cm, in each experimental unit to measure soil matric potential.

Soil water regime treatments. Beginning 29 October 1978, three treatments were applied to randomly selected experimental units in 4 replications. Soil matric potential was measured three times weekly, and water was applied to bring the soil to field capacity each time gypsum blocks indicated an average −1, −7, or −15 bar matric potential at the 20 cm depth, for the three treatments, respectively. The treatments closely simulated field conditions recorded by Evans et al. (1975). After 15 March 1979, two of the four replicates for each treatment were allowed to dry, simulating an early end of the winter rainy season. The remaining two replicates continued under the original treatments until 19 May 1979, when the plants began to senesce.

Plant sampling. On 11 November 1978, five plants each of *Bromus mollis* and *Avena barbata* were marked in each experimental unit. Maturing panicles on the marked plants were enclosed in translucent paper bags on 12 May 1979 to collect developing seeds.

The collected seeds were counted, weighed, and then stored in the laboratory until 11 December 1979, when seeds from each plant were germinated separately in greenhouse flats. A mixture of sand and peatmoss (U.C. soil mix) was used as a germination substrate, with sand sprinkled over the seeds. Distilled water was applied as needed until 20 March 1980. As seedlings emerged, they were counted and discarded; emergence was taken as a measure of successful germination.

In June 1979, fifty seeds of each species were selected at random from each water regime treatment. Average seed weight was recorded before sowing the seeds in boxes with slanted plate glass fronts. Plant height and root length were measured five days after germination. Rooting space was limited so three groups of seeds were planted sequentially in the boxes: all the −15 bar treatment seeds were grown together, followed by the −1 bar treatment seeds, and then the −7 bar treatment seeds. Comparison of seedling top and root growth was made only among seedlings growing in the same box and the same trial.

In the text, a significant difference is indicated when sample means, by an F-test, have a less than 5% probability of being equal ($p < 0.05$). A highly significant difference occurs when $p < 0.01$. Bars in histograms topped with the same letter are probably not different ($p < 0.10$).

Results

Seed production. When water was available throughout the growing season, maximum seed production for *B. mollis* occurred under the −1 bar treatment (Fig. 1A). The −7 bar conditions reduced seed production, which was further reduced by the −15 bar regime. Water withheld after 15 March sharply reduced *B. mollis* seed production from that in the −1 and −7 bar "dried late" treatments. The decrease appeared to be much less under the −15 bar conditions. On the average, the number of seeds produced by plants in the "dried early" treatments were significantly fewer than those produced in the "dried late" treatments. *Avena barbata* responded similarly to the water regime treatments (Fig. 1A). When water was available throughout the growing season, maximum seed production occurred under the −1 bar treatment. Seed production was reduced by the −7 bar regime and further reduced under the −15 bar conditions. Early depletion of

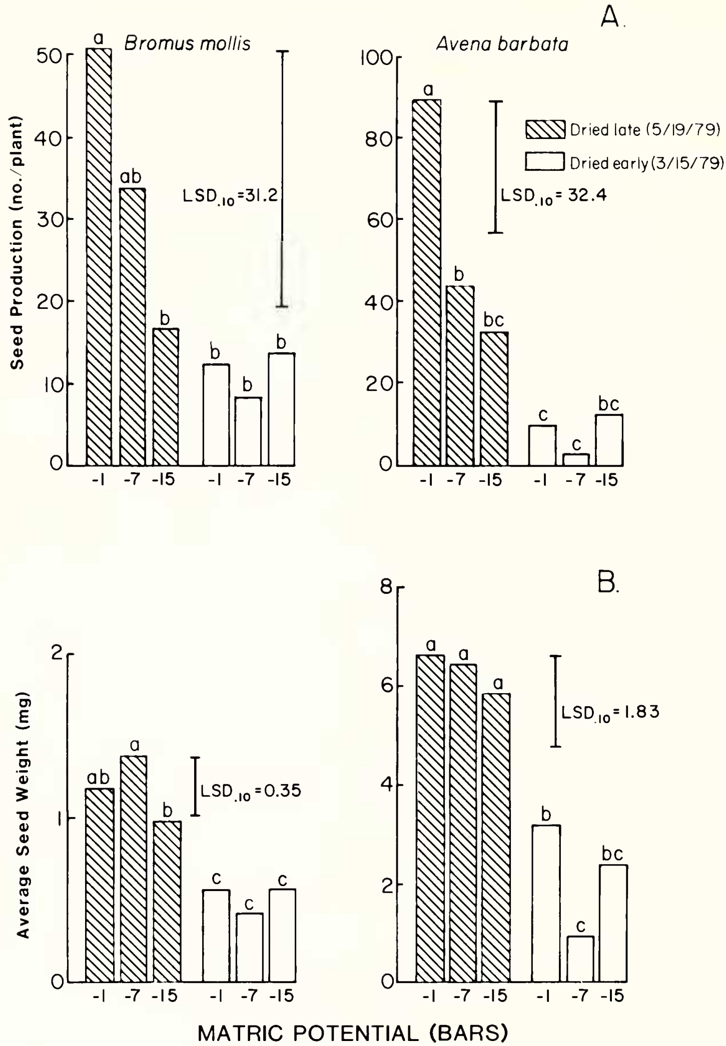

FIG. 1. Number and average weight of seeds (florets) produced by *Bromus mollis* and *Avena barbata* plants dried early or late and growing in three soil water regime treatments (−1, −7, −15 bars). Bars labeled with the same letters are not significantly different at the 10% level.

available soil water (no water after 15 March) greatly reduced seed production in all treatments and, again, the least decrease occurred in the −15 bar treatment. Differences between the "dried early" and "dried late" treatment groups were highly significant.

Seed weight. The effect of periodic drought during the growing season on average *B. mollis* seed weight is not clear (Fig. 1B). A slight reduction was observed under the −15 bar treatment. Although seed numbers were reduced, average seed weight was relatively uniform if water was applied until 19 May. A significant reduction in seed weight occurred when water was withheld after 15 March, the average seed weight being 55% less. *Avena barbata* seed weights were relatively uniform with periodic drought during the growing season (Fig. 1B) even though seed numbers were reduced. Seed weights did not differ among treatments when water was available through 19 May, but significant differences occurred when the soil dried early. On the average, withholding water after 15 March reduced seed weight by 79%.

Reproductive potential. Periodic drought during the growing season did not affect germination rate of *B. mollis* seeds (Fig. 2A). About 50% germination occurred in seeds produced by plants growing in both the −1 and −15 bar treatments if water was available through 19 May. Only prolonged spring drought resulted in significant germination rate reductions. While moderate decreases in germination rate may have occurred under the more intense drought treatments, neither periodic drought during the growing season nor early depletion of soil water reserves significantly reduced the percentage of *A. barbata* seeds that germinated (Fig. 2A).

The reproductive potential of a plant is more accurately represented by the number of germinable seeds produced. Periodic drought during the growing season reduced reproductive potential of *B. mollis* (Fig. 2B). Plants undergoing the −1 bar treatment produced more germinable seeds than plants undergoing the −7 bar and −15 bar treatments. A highly significant reduction occurred when water was withheld after 15 March, and the reproductive potential of plants in the −15 bar treatment was reduced by 41%. For the −7 bar and −1 bar treatment plants, 93 and 85% reductions occurred, respectively. Though not all marked *B. mollis* plants reproduced, at least some germinable seed was produced in each experimental unit. Reproductive potential of *A. barbata* was also reduced by periodic drought during the growing season (Fig. 2B). Plants growing under the −1 bar treatment produced many more germinable seeds than plants growing in the −7 bar and −15 bar treatments. Withholding water after 15 March further reduced reproductive potential and was probably more critical because a 71% reduction occurred in plants already receiving the −15 bar treatment. Early depletion of soil water reserves significantly reduced reproductive potential, 96 and 90% in the −7 bar and −1 bar treatments, respectively. Nevertheless, some germinable *A. barbata* seed was produced regardless of soil water conditions.

Second generation seedlings. Seeds produced by plants grown under the various soil water regimes were planted to determine whether

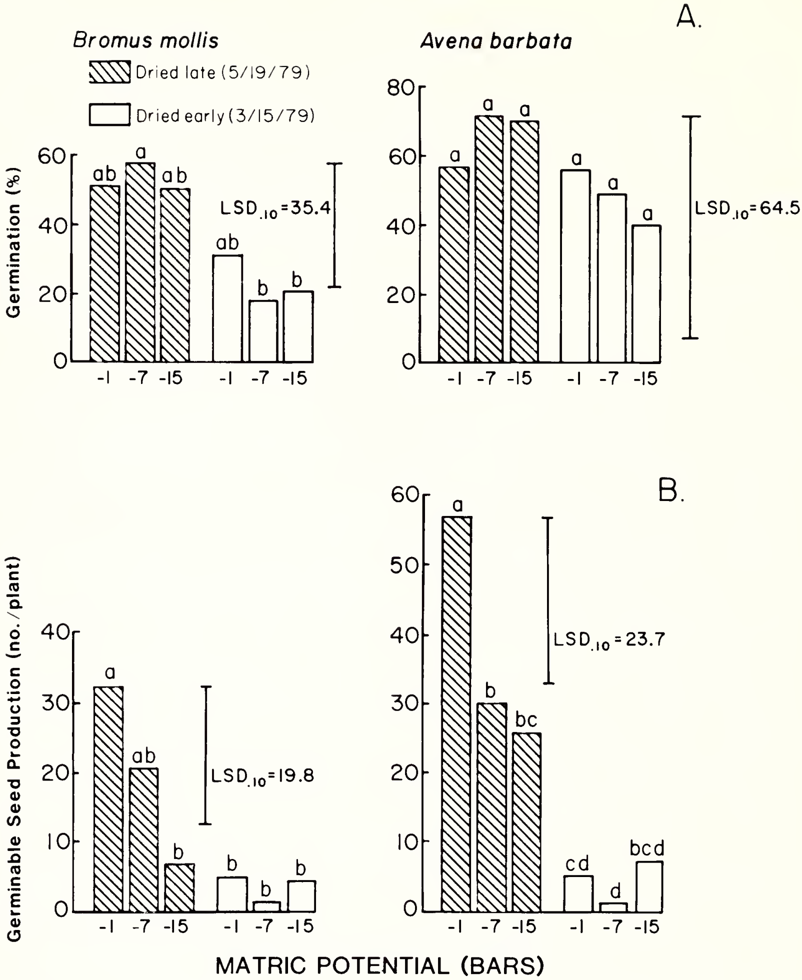

FIG. 2. Germination rate and number of germinable seeds produced by *Bromus mollis* and *Avena barbata* plants dried early or late and growing in three soil water regime treatments (−1, −7, −15 bars). Bars labeled with the same letters are not significantly different at the 10% level.

the subsequent generation of seedlings reflected stress on parent plants. Average weight was lower for seeds taken from "dried early" treatments (Table 1). In all instances, smaller seeds from stressed parent plants produced significantly smaller seedlings. For example, *B. mollis* plants receiving the −15 bar treatment produced seeds weighing on the average 2.2 mg if water was applied through the spring. Five day

TABLE 1. AVERAGE WEIGHT OF SEEDS PRODUCED BY PLANTS GROWING IN SIX SOIL WATER REGIME TREATMENTS AND SUBSEQUENT SEEDLING SIZE (5 DAYS AFTER GERMINATION). "Early" means water withheld after 15 March; "Late" means water applied until 19 May.

Treatment	Ave. seed weight (mg)	Ave. seedling height (mm)	Ave. root length (mm)
Bromus mollis			
−1 bar early	1.5	26	40
−1 bar late	2.4	34	58
−7 bars early	1.5	20	34
−7 bars late	2.5	28	52
−15 bars early	1.2	19	60
−15 bars late	2.2	40	94
Avena barbata			
−1 bar early	6.4	53	65
−1 bar late	8.5	62	84
−7 bars early	6.7	38	64
−7 bars late	10.8	47	80
−15 bars early	5.8	45	98
−15 bars late	7.8	57	130

old seedling height from those seeds averaged 40 mm and root length averaged 94 mm. *Bromus* plants receiving the −15 bar treatment and early spring drought produced seeds weighing 1.2 mg on the average (46% reduction). Seedling height from those seeds averaged 19 mm (52% reduction) and root length averaged 60 mm (36% reduction). Water stress decreased reproductive output of plants growing under all water regimes. Water stress on the parent plant also decreased seedling size of the next generation.

DISCUSSION

Reproductive output of *B. mollis* and *A. barbata* was reduced by periodic drought during the growing season. Maximum seed production occurred only when water was readily available over the entire growing season. A simulated end of the rainy season in mid-March greatly reduced seed production but never completely suppressed it. Given the data of Evans et al. (1975) showing only rare soil water potentials below −10 bars, in many annual grassland areas it is unlikely that drought conditions occur that would completely interrupt or stop seed production.

Bromus mollis and *A. barbata* are ideally suited to the Mediterranean climate in California because they survive the dry summer season as seeds. They are also suited because even under extreme drought conditions, at least a few germinable seeds are produced to carry the species through the summer.

When plants experienced short drought periods during the growing season, seed numbers were reduced but seed weights and germination rates stayed relatively uniform. Stressed plants allocated energy to fewer seeds and maintained reproductive efficiency of those seeds. Only when drought stress was severe and prolonged during spring did seed weights and germination rates decline.

Drought stress resulted in smaller as well as fewer seeds, and smaller seeds produced smaller seedlings. Seedlings from small seeds may be at a competitive disadvantage in a mixed stand (Black 1958). Through changes in seed production, seed size, and seedling vigor, there is a possibility that annual vegetation reflects not only the current year's growing conditions but also the previous years'. Future experiments with annual grassland species and communities should take this into account, especially when seeds of unknown origin are used.

One of the problems encountered in evaluating the data was tremendous variation in the number of seeds produced by a single plant. While this type of variation is distressing for the researcher, it may well be adaptive for the species, enabling at least some members of the population to survive year-to-year environmental variation.

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